ONION IMPROVEMENT

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THE onion is used as a food and for seasoning in nearly all countries, and its culture no doubt dates back to very remote antiquity. According to Sturtevant, as reported by Hedrick (*9*),[1] it is—

> One of the things for which the Israelites longed in the wilderness and complained about to Moses. * * * Onions were prohibited to the Egyptian priests, who abstained from most kinds of pulse, but they were not excluded from the altars of the gods. * * * They were introduced at private as well as public festivals and brought to the table. The onions of Egypt were mild and of an excellent flavor and were eaten raw as well as cooked by persons of all classes.

ORIGIN, CULTURE, AND USES

BAILEY (*2*) describes eight species of onions cultivated in North America. *Allium neopolitanum* Cyr. and *A. moly* L. are grown as ornamentals. Garlic (*A. sativum* L.) is used mainly for seasoning. The leek (*A. porrum* L.), the Welsh or Japanese onion (*A. fistulosum* L.), and the shallot (*A. ascalonicum* L.) are all used in the green condition. The tops of chives (*A. schoenoprasum* L.) are used for seasoning. *A. cepa* L. is the species cultivated most extensively. Bailey divides this species into several botanical varieties as follows: (1) The extensively cultivated bulbing type of onion propagated by seed; (2) the potato or multiplier onion, which propagates by branching at the base; and (3) the top onion, which forms bulbils in the inflorescence, which are often used for propagation.

Vavilov (*21*) names the middle-Asiatic center, comprising northwestern India, all of Afghanistan, the Soviet Republics of Tajik and Uzbek, and western Tien Shan, as the primary place of origin of the commonly cultivated onion, *Allium cepa*. As secondary centers of origin of this species he lists (1) the Near East, which includes inner Asia Minor, the whole of Transcaucasia, Persia (Iran), and the alpine Turkmen Republic, and (2) the Mediterranean region. For the Japanese onion, *A. fistulosum*, which is cultivated extensively in the Orient, Vavilov gives the primary place of origin as the Chinese center, which comprises alpine central and western China and the adjacent lowlands.

From these centers of origin the onion has spread to all countries where the crop can be grown at some season of the year. Just when the cultivated onion was first introduced into North America is not known, but at present it is cultivated everywhere in this country as a

[1] Italic numbers in parentheses refer to Literature Cited, p. 249.

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home-garden and market-garden crop. Extensive commercial production, however, is confined to special regions.

The early crop for shipment is grown chiefly in Texas, California, and Louisiana from transplanted plants set in the field in late fall and early winter and harvested the following April, May, and early June. The predominant variety is Yellow Bermuda, but Crystal White Wax and Creole are also grown to a considerable extent. These varieties are used for the early crop because they produce bulbs during the time of the year when the days are short. The Bermuda type cannot be stored successfully for more than a few weeks, but Creole is a good storage onion.

The intermediate crop is grown primarily in Texas, New Jersey, California, Oklahoma, Washington, and Iowa from transplanted seedlings and from dry sets, the crop being harvested chiefly during June and July. In Texas the principal intermediate variety is the Yellow Bermuda; in California, the Stockton Yellow Globe and California Early Red; in Iowa, the Yellow Bottleneck; in the East, the Ebenezer, Yellow Strasburg, and others of the same type. In Texas and California the intermediate crop is grown from transplants; in other districts dry sets are used.

The late or main crop, which is produced chiefly in Michigan, New York, Indiana, California, Ohio, Massachusetts, Colorado, Minnesota, Idaho, Oregon, Washington, Wisconsin, and Utah, is usually seeded directly in the field and harvested in August and September. This crop, most of which is stored, supplies the demand from September until late March or April. Storage varieties are not

OFTEN *an onion crop that might have been a profitable one brings the grower a loss because of unfavorable weather conditions and the occurrence of certain insect pests and diseases that take their toll in both field and storage. Smut occurs in practically all of the main onion-growing States of the North, while pink root is present in most of the onion districts of the South and West. Onion thrips are always present on both the bulb and seed crop. Smudge, neck rot, and other diseases take an additional share of the crop after harvest. Other losses occur because of premature seeding in the field and sprouting in storage. Until very recently, little has been done to alleviate these difficulties by scientific breeding methods. Present researches and experiments, however, make the possibility of preventing many such losses by developing superior varieties of onions more and more promising. In most cases resistant varieties and strains have been found, and in some cases promising hybrids have been produced and are under test.*

the same for all sections. In California, Australian Brown is used; in Oregon, the Oregon Danvers; in the Rocky Mountain States, Sweet Spanish and Mountain Danvers, and in the Northern States from Minnesota to Massachusetts, the yellow globe type such as Yellow Globe Danvers, Southport Yellow Globe, and Ohio Yellow Globe. Other varieties stored to some extent are Southport Red Globe, Southport White Globe, Red Wethersfield, White Portugal, Ebenezer, and Yellow Strasburg. With the exception of Sweet Spanish, these storage varieties are rather pungent.

During seasons of low production imports have been chiefly from Spain, Egypt, Chile, Italy, and Canada.

The quantity of onions consumed per capita in the United States is fairly constant regardless of price. During years of overproduction a portion of the crop is usually plowed under, and during years of underproduction imports are increased. The onion market is not very elastic, oversupplies are not readily absorbed, and consequently it is rather easy to have overproduction. As a rule, onions are used by most families in comparatively small quantities but fairly constantly throughout the year for seasoning, in salads, and as a main dish cooked in a variety of ways. Onion salt is also being manufactured in considerable quantities for use in catsup, chili sauce, soups, and sausage. But while the quantity of onions consumed per capita is not large, the total amount used gives this crop a commercially important place among the vegetables. The average onion acreage for the United States during the 5-year period 1928–32 was 84,430 acres, with a production of 13,247,000 100-pound sacks, giving a yearly return to the producers of approximately $17,353,000.

VARIETAL ADAPTATION

Among the onion varieties grown in the United States there are many types differing in size, shape, and color of bulbs, pungency, keeping quality, time of maturity, and tolerance to diseases, insects, sunscald, and high and low temperature. It has been necessary to maintain a considerable number of varieties, partly because of consumer demands relating to season and use, but chiefly because of the different environmental conditions under which the crop is grown. The storage onions of the North, for example, do poorly in the South, and the extra early varieties commonly grown in the South are ill-suited for production in the North.

The adaptability of varieties to certain regions, according to Magruder and Allard (*14*), is often determined by length of daylight, called the photoperiod. The time when bulbing is initiated is determined by the length of the photoperiod and not by the age of the plant, and the minimum photoperiod necessary to initiate bulbing varies with different varieties. The investigators named above were able to group the varieties into classes according to the minimum photoperiod required to produce 100 percent normal bulbs as follows: 12 hours, Yellow Bermuda, White Creole, and Early Grano; 13 hours, California Early Red, Yellow Strasburg, Ebenezer, and Yellow Danvers Flat; 13.5 hours, Early Yellow Globe, Mountain Danvers, Ohio Yellow Globe, Australian Brown, White Portugal, Southport Yellow Globe, and Sweet Spanish strain no. 1; 14 hours, Red Wethersfield, Southport Red Globe, and Italian Red; 14.25 hours, Yellow Globe Danvers; normal day (maximum of 14.9 hours), Sweet Spanish strain no. 2. Most commercial varieties are not homozygous or pure for the genes that determine the minimum photoperiod for bulbing, so there may be some plants that bulb at a shorter photoperiod than is characteristic for the variety.

Early maturity, according to Magruder and Allard, seems to depend on the ability of the plant to start bulb formation at short photoperiods and to proceed very rapidly with the process after the minimum period for bulbing is reached. In the North it is almost impossible to secure good yields of the extra early varieties like the Bermudas, Early Grano, and Creole by sowing seed directly in the field, because seeding is usually done at a date when the length of day has already passed the minimum for bulbing. Consequently the plant develops only a few leaves and a small bulb. To secure large bulbs of the extra early varieties in the North it is necessary to sow seed early in a greenhouse or in a hotbed in order to have large plants before the minimal photoperiod for bulbing occurs.

The late-maturing varieties of onions usually do poorly in the South, chiefly because the photoperiod required for bulbing comes during hot weather, when sunscald, thrips, and pink root combine to retard the growth of the plant. Lateness of maturity, according to Magruder and Allard, may be due to a long photoperiod requirement, to a slow rate of bulb development after the minimum occurs, or to a combination of the two. Sweet Spanish, a late variety, is able to produce fair crops in the South because it is somewhat resistant to sunscald, thrips, and pink root.

In central California there is a considerable acreage of the so-called intermediate crop of onions. The seed is usually sown in field beds in late August and the seedlings are transplanted in late November and December. During the winter and early spring the plants usually make a large vegetative development. Bulbing does not begin in the spring until the hours of daylight reach the minimum for the varieties in question. For this crop, varieties such as Stockton Yellow Globe, California Early Red, and Italian Red are used. If the late varieties of the North or the early varieties of the South are used they make a good vegetative growth, but in the spring the plants form seed stems instead of bulbs.

These few points regarding adaptation are brought out to show why a variety may do well in one district and be worthless in another. Sweet Spanish is much more widely adapted than many varieties because of its resistance to high temperature conditions and to certain insects and diseases. Other varieties will be more widely adapted when plant breeders incorporate in them genes for resistance to diseases and insects and others that permit them to grow under a wider range of climatic conditions.

INTRODUCTION OF PRESENT COMMERCIAL VARIETIES

It is difficult to obtain authoritative information on the method and time of introduction of the older important commercial varieties. the first mention in seed catalogs of certain important varieties is as follows: Silverskin (White Portugal), 1810; Crystal Wax, 1901; Red Wethersfield, 1849; Ohio Yellow Globe, 1901; Southport Red

Globe, 1889; Southport White Globe, 1889; Southport Yellow Globe, 1888; Yellow Danvers (Flat), 1866; and Yellow Strasburg, 1844. According to Morse (*17*), the variety Australian Brown was introduced into North America from Australia in 1894, under the name of Brown Spanish, but later was renamed by W. Atlee Burpee. An improved strain, Australian Brown U. C. No. 1, was introduced by the California Agricultural Experiment Station in 1935. Sweet Spanish seed was secured by the United States Department of Agriculture from Luis Tono, American consul in Spain, in December 1908, under the name of Denia, and was distributed to seedsmen and several agricultural experiment stations. An improved strain, Sweet Spanish Colorado State No. 6, was introduced by the Colorado Agricultural Experiment Station in 1936. According to Morse (*17*), Prizetaker was first offered to the trade in America by William Henry Maule in 1888, from seed grown by C. C. Morse the preceding year at Santa Clara, Calif. In Europe this variety was known as Spanish King. The Early Grano onion, named and introduced by the New Mexico Agricultural Experiment Station (*8*), was secured from Spain in 1925 under the name of Valencia Grano by the Barteldes Seed Co., of Lawrence, Kans.

Morse (*17*) states that the California Early Red has been developed from the Red Italian Tripoli. The latter was probably brought to California by the early Italian emigrants before 1900. An improved strain, California Early Red, U. C. No. 1, was introduced by the California Agricultural Experiment Station in 1935. The variety Stockton Yellow Globe was originated by a number of American and Japanese growers in California in response to a demand for a nonbolting yellow globe onion; consequently there are a number of strains of this variety, the type of which has not as yet become definitely established. According to Erwin and Harter (*6*), the parent stock of Yellow Bottleneck was "Birn Zwiebel" and was secured from Germany in the late sixties by a Mr. Lafrenz, of Davenport, Iowa. The Creole variety was probably brought to Louisiana by the early French settlers. Yellow Bermuda (formerly called White Bermuda) was probably introduced from the Canary Islands some time prior to 1901.

VARIETAL IMPROVEMENT

Often an onion crop that might have been a profitable one brings the grower a loss because of unfavorable weather conditions and the occurrence of certain insect pests and diseases that take their toll in both field and storage. Smut occurs in practically all of the main onion-growing States of the North, while pink root is present in most of the onion districts of the South and West. Onion thrips are always present on both the bulb and seed crop. Smudge, neck rot, and other diseases take an additional share of the crop after harvest. Besides these, other losses occur because of premature seeding in the field and sprouting in storage. Little has been done until very recently to alleviate these troubles by scientific breeding methods. Hope of preventing many losses in the future by developing varieties resistant to various insects and diseases and certain unfavorable climatic conditions seems more and more promising. Some of the work actually under way is described in later sections of this article.

Commercially Maintained Seed Stocks

To give a comprehensive idea of onion improvement as it is being conducted at present, it will be necessary to review methods employed by commercial interests as well as by State and Federal investigators. Most of the onion seed produced at the present time is grown in California. There the mother bulbs of the different varieties are grown like those for market, with the exception that the rate of planting is heavier so that the plants are more crowded and a somewhat smaller bulb is produced. These are grown by contract at so much per 100-pound bag. Harvesting is usually done in August and September, and the bulbs remain in the bag until time to plant in the field in late November or December. Before planting, most seedsmen pass the mother bulbs over a grading table to sort out the off-color ones and at the same time select mother bulbs of good type to plant for the production of stock seed. As a rule, the bulbs of the various varieties are distributed to ranchers who contract to grow the seed at so much per pound.

If mother bulbs are selected carefully, it is possible to maintain fairly uniform stocks of the different varieties. Onions, however, are highly cross-pollinated, and commercial varieties have a very mixed heredity. Usually there are enough differences between the plants of a variety so that it is possible to select rather widely for type. It is seldom that any two people have exactly the same idea of what the type should be in making selections. As a consequence there are many strains of each variety. Also, by following the selection method exclusively certain recessive colors and off-types are never bred out; they are carried along indefinitely. Progressive seedsmen, however, are beginning to use scientific methods to develop strains that are more uniform in size, shape, and color. Breeding for the development of resistance to diseases and insects, however, is being conducted chiefly by the Federal Government and by the State-supported research institutions. To understand these methods better it is well to know something about the flowering habit and the floral characters of the onion plant.

Inflorescence and Pollination

When mother bulbs are planted in the late fall or winter the rudimentary parts of the flower stalks do not differentiate until the following spring, and it is usually 3 or 4 weeks after differentiation before the flower parts emerge through the sheaths that surround them. The flower stem elongates rapidly and may develop to a height of 5 or 6 feet but usually not more than 3 or 4 feet. The number of flower stems per plant ranges from 1 to 20 or more, depending on the size of mother bulb, the variety, and climatic conditions.

The flowers are borne in simple umbels at the upper end of the elongated stalk, the young buds being enclosed within a papery bract which is split open by pressure of the developing buds shortly before the flowers open. The number of flowers per umbel may range from 50 or less to 2,000 or more. The flowers have six perianth lobes or floral leaves in two whorls of three each and six stamens in two whorls of three each. The pistil has a three-celled ovary with two ovules in each cell. The anthers of the three inner stamens are the first to open, shedding their pollen one after the other at irregular intervals, after which the anthers of the outer whorl of stamens open, also at irregular intervals (fig. 1). The pollen of a single flower is shed before the stigma becomes receptive, and the process is usually completed in 24 to 36 hours. The style is approximately 1 mm (0.039 inch) long when the flower first opens, not reaching its maximum length of about 5 mm (0.197 inch) until a day or two after all the pollen from that flower has been shed. The flowers of a single head may continue to open over a period of 2 weeks or longer, and a plant may be in flower for 30 days or more.

Most of the pollen is shed between 9 a. m. and 5 p. m. Pollination is effected mainly by insects that go from flower to flower and visit the nectaries at the base of the three inner stamens. Interpollination among flowers of the same umbel is no doubt of frequent occurrence, as the same insect has been observed to visit many flowers on an umbel before leaving. In the onion, however, cross-pollination is the rule.

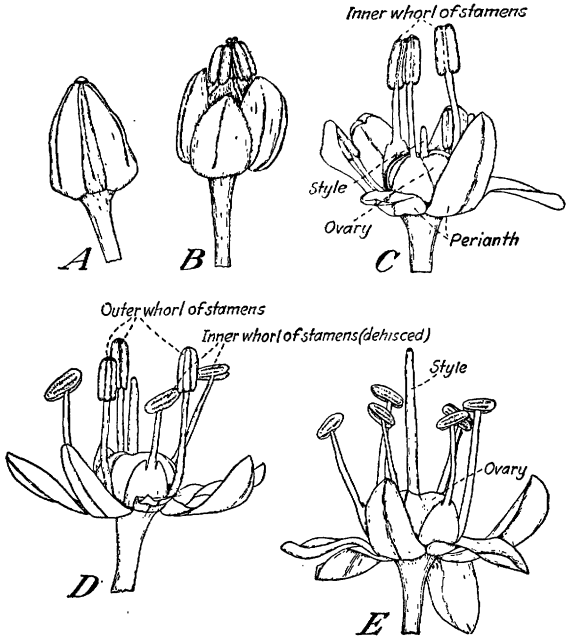

Figure 1.—Method of flower opening and pollen shedding in the onion: *A*, Flower bud just before opening; *B*, the two outer whorls of floral organs expanding and the inner whorl of stamens elongating; *C*, just before the shedding of the pollen by the inner whorl of stamens; note the short style; *D*, the three stamens of the inner whorl have shed their pollen and the three of the outer whorl have elongated; *E*, all six stamens have shed their pollen; note the long style, now receptive. (From Jones and Rosa, *Truck Crop Plants.*)

Selfing an Aid in Onion Breeding

In the onion selfing or inbreeding, accomplished when a plant is self-pollinated, is not an end in itself but merely one of the tools used in the breeding program. Inbreeding in the onion is almost always accompanied by a loss of vigor for a number of generations. However, it permits many undesirable characters that have been carried along in the germ plasm, perhaps covered up by dominant traits, to express themselves, so that the lines possessing them can be rogued out. The main purpose of inbreeding is to develop lines that will breed true for certain characters. Selfing is accomplished in the onion by covering the entire umbel to prevent contamination with foreign pollen. When the first flower opens on an umbel the entire inflorescence is enclosed within a 1-pound manila paper bag and tied closely so that there will be a crowding of the flowers within the bag (fig. 2). If the umbels are small, as is usually the case after several generations of inbreeding, a number of heads can be enclosed in the same bag, thereby crowding flowers and facilitating pollination. Once each day toward evening, when the pollen is dry, the bags are tapped rather vigorously to help circulate the pollen within.

Breeding Program with Inbred Lines

Much of the improvement work, especially by commercial seedsmen, has as its object the freeing of varieties from plants that are off-type and making a variety or strain uniform for important commercial

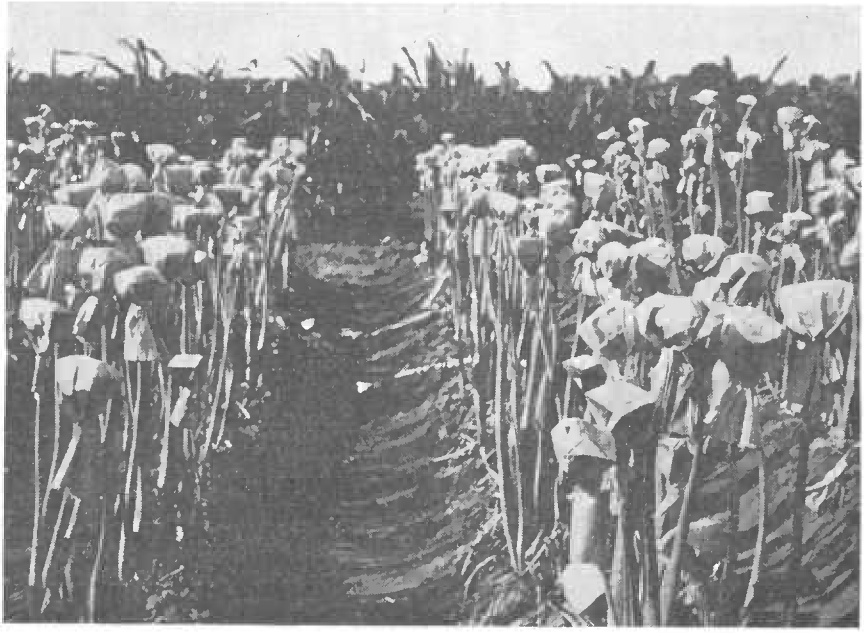

Figure 2.—**Method of self-pollinating onions. Inflorescences are enclosed in 1-pound manila paper bags.**

characters. This can best be done by selecting bulbs that are true to type, selfing to secure uniform and true breeding lines, and finally massing the apparently similar selected inbred lines to bring about crossing, which will restore vigor. Such a program follows:

First year.—Select a large number of commercial bulbs that approach the ideal for the variety; the larger the number the better the chance of securing desirable lines. Plant the selected mother bulbs in late fall, winter, or early spring, depending upon the locality.

Second year.—Self-pollinate as described in the section on selfing.

Third year.—Grow progenies of all selfed plants separately. Destroy undesirable lines during the growing season, or at harvest time, or upon their removal from storage. Retain the best bulbs in 25 or more of the most outstanding lines and plant for selfing and open-pollination.

Fourth year.—Half of the umbels on each plant are selfed and the others are allowed to open-pollinate. By following this procedure it is possible to secure a supply of open-pollinated seed of superior quality that can be increased rapidly to quantity production. For practical purposes it is usually best not to inbreed more than two generations, because as a rule the plant is greatly weakened and it is difficult to secure a quantity of seed.

Fifth year.—Grow the progenies that were selfed in the fourth year separately and again select the best bulbs from at least 25 lines for open-pollination.

Sixth year.—Group all selections and plant them in the field so that the maximum amount of crossing between unrelated lines will occur. Mass the seed and increase.

Use of Flies to Facilitate Crossing

When new characters are to be incorporated in a variety, as is necessary in most cases when breeding for disease resistance, then the breeder must resort to crossing. Plants to be used for crossing are

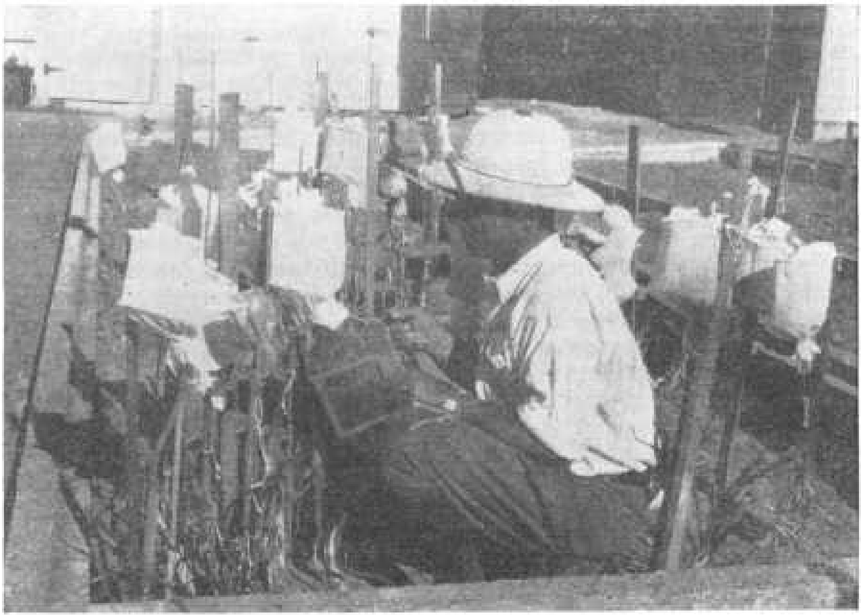

Figure 3.—Method of introducing flies into small pollination cages. The cages are made of cheesecloth stretched over wire frames and tied at both ends. (Courtesy California Agricultural Experiment Station.)

usually set 2 to 3 feet apart in the row to allow plenty of room for manipulation of the small cage to be described later. The umbels are bagged as soon as the first flower opens. At first only a few flowers on an umbel open daily, but the number increases until full bloom, when 50 or more may open in a single day. These early flowers are removed several times daily from the umbel of the female parent. When the weather is hot they must be removed often because the anthers shed their pollen very soon after a flower opens. When blossoming is at its peak, open flowers are no longer removed but are emasculated and used for crossing. Umbels must be examined frequently and the anthers removed from the open flowers before the pollen is shed to prevent contamination of the umbel.

When enough flowers have been emasculated, the remaining buds of the inflorescence are removed. The emasculated and disbudded umbel is then enclosed under a small cheesecloth cage as shown in figure 3. The inflorescence of the male, or pollen, parent, which has also been kept covered to prevent pollen contamination, is cut off and enclosed within the same cage, with the base of the stalk standing in a bottle of water. When handled in this manner the flowers continue to open and shed pollen for a week or more. Flies are added to the cage to do the pollinating. This technique, as compared with hand-pollination, makes it possible to multiply greatly the number of crosses, and also to secure a higher percentage of seed setting. To be certain that flies are free from foreign pollen, it is necessary to raise them under controlled conditions.

At Davis, Calif., where considerable onion-breeding work is under way, a technique for the growing of flies for pollination purposes has been developed. Lungs of beef, upon which the adult blowflies lay their eggs, are exposed on tables in the open. The lungs are under a roof to provide protection from a high temperature and rain, which might kill many of the larvae. Within a few days the larvae hatch and begin to feed. When mature they begin to wander about to find a place to pupate, at which time they are trapped by attaching a trough along the side of the table into which the larvae fall. A pail, containing a small amount of finely screened sand, is suspended at the end of the trough. Once each day the pail is removed and replaced by another so that each pail will contain larvae of approximately the same age. The larvae soon burrow into the sand to pupate, and later the pupae are separated from the sand by screening. The pupae are held at room temperature and are placed in a small screen cage before the adults emerge (fig. 3). Each cage, measuring about 6 by 6 inches, has a cone-shaped top, at the apex of which is a small opening closed by a cork. As the flies hatch they gradually move up into the cone. When used in pollinating, the cone is inserted into the lower end of the cloth cage containing the two umbels, the cork is removed, and as many flies as needed are allowed to escape into the cage. They soon begin to feed and in doing this carry pollen from flower to flower and accomplish pollination.

It is often desirable to accumulate mature pupae in order to have a good supply on hand for the peak of the pollinating season. They can be kept for several weeks at about 45° F. It is best not to store them at this temperature until the adults are almost ready to emerge, otherwise fewer of them will emerge. Also, the flies appear to be less active when the pupae are stored early in the pupation period.

BREEDING FOR RESISTANCE TO DISEASE

PINK root of onion, caused by the fungus *Phoma terrestris* Hansen, is a major disease in many onion-growing districts, especially of the South and West. Porter and Jones (*18*), working in California, found that Sweet Spanish was slightly resistant to pink root and that the Japanese onion, *Allium fistulosum*, Nebuka type, was very resistant. In California, Australian Brown No. 17, a single plant selection, is somewhat more resistant than the commercial variety from which it was isolated, and Sweet Spanish No. 35, another single plant selection, is also more resistant than the commercial variety. Felix (*7*) has also reported that Winterhecke and White Welsh, varieties of *A. fistulosum*, as well as different strains of Nebuka (Natsu-negi Nebuka, Senj-negi Nebuka, Tokyo-Nebuka, and Iwatsuki), are resistant to pink root.

The various types of *Allium fistulosum* have little commercial importance in the United States, but it would be desirable to have certain insect- and disease-resistant characters they possess incorporated in varieties of *A. cepa*. With these objects in view, Emsweller and Jones (*3*) have made a large number of crosses between some of the Nebuka types and many varieties of *A. cepa*. First-generation hybrids of Yellow Globe Danvers × Nebuka and Nebuka × Australian Brown have been grown on soil heavily infested with the pink root organism; the roots showed some pink, but the plants apparently were not checked in their growth. The Australian Brown variety has proved very susceptible to pink root, yet the hybrid grew vigorously on infested soil throughout the season. Back crosses have been made to the Australian Brown variety, but readings have not as yet been made on resistance.

The smut disease, caused by the fungus *Urocystis cepulae* Frost, is present in most of the onion-growing districts of the North. Formaldehyde applied in the row at time of seeding is a satisfactory control measure, but the cost of this treatment could be eliminated by the development of resistant varieties. In 1925 Anderson (*1*) suggested the use of Winterhecke as the logical parent for the breeding of a smut-resistant onion by crossing. He states that it is almost immune to smut, and by his description of the variety one is led to believe that it is the Nebuka type of *Allium fistulosum*. In 1932 the writer sent seed of the Nebuka to A. G. Newhall, of Cornell University, who tested the seedlings under epidemic conditions and found them to be practically immune to smut. Breeding work is under way at present looking toward control by the use of resistant varieties. Progenies involve crosses between the two species, *A. cepa* and *A. fistulosum*. Only a few first-generation hybrid plants were secured, and these have been self-sterile. Back crosses have been made to both parents, however, but as yet these progenies have not been subjected to resistance tests.

Mildew, caused by the fungus *Peronospora schleideni* Unger, is one of the most destructive diseases to the onion seed crop. In California losses may run as high as 80 percent in some seasons. Several onion strains that are highly resistant to mildew have been isolated by investigators of the California Agricultural Experiment Station. One of these is a male-sterile strain of Italian Red, pedigree 13–53, the leaves of which are highly resistant and the seed stems apparently immune. Many progenies are now being tested under epidemic conditions.

A disease called smudge, caused by the fungus *Colletotrichum circinans* (Berk.) Vogl., does considerable damage to the storage crop of the North by causing bulb shrinkage and premature sprouting. Walker, Link, and Angell (*23*) have shown that pigmented varieties of onions are resistant to smudge, while the white are not. On pigmented onions the disease is confined mainly to the neck. Resistance is probably due mainly to the presence of protocatechuic acid—one of the carbolic acids—which is in some way closely associated with the yellow and red pigments in the dry outer scales of the bulb. Insofar as known, this is the first case where resistance to a certain disease has been shown to be due to a definite chemical constituent. Rieman (*20*), in a study of the relation of pigmentation to disease resistance, states that the genes *W* (red) and *Wy* (yellow), which are responsible for the production of the red and yellow pigments, are also responsible for the production of protocatechuic acid. Whether or not resistance can be incorporated in the true-breeding white varieties of onions remains to be determined.

According to Walker (*22*), pigmented onions are also more resistant to the invasion of certain species of the fungus *Botrytis* (*B. allii* Munn, *B. squamosa* Walker, and *B. byssoidea* Walker). He states that resistance in colored bulbs appears to be due to a water-soluble toxic substance in the outer scales that excludes the fungi. Colored bulbs are not resistant once infection is established.

Yellow dwarf is a virus disease of onion that causes a characteristic yellowing, wrinkling, twisting, and drooping of the leaves and dwarfing of the plant. This disease was prevalent for a time in the Pleasant Valley onion district of Iowa and has also been reported in other districts. In a field test of 34 varieties in 1929 Henderson (*10*) found that Sweet Spanish was the only variety showing marked resistance. Plants of this variety did not contract the disease when inoculated artificially and furthermore did not carry the disease in a masked form. It will be recalled that this same variety carries considerable resistance to thrips and to pink root.

BREEDING FOR RESISTANCE TO INSECTS (THRIPS)

Thrips are present wherever onions are grown, and it is estimated that they cause more loss than all other insect pests and diseases combined. Satisfactory chemical control has thus far been impossible, because a large number of thrips are always protected between the inner leaves of the plant, the pupal stage is spent in the soil, the species is very prolific, the generations overlap, natural parasites are lacking, and other host plants are numerous. The unsatisfactory control secured by chemical means necessitates a mode of attack different from that made in the past. Jones, Bailey, and Emsweller (*11*) showed that certain varieties and species of onion have definite resistance to thrips. Among the most resistant are White Persian, Nebuka, California Early Red, Early Grano, and Sweet Spanish. Counts made in 1932 and 1933 showed that the varieties used were resistant in about the same order in both years, so that certain of their characters evidently influenced the size of the thrips population per plant.

The White Persian variety (P. I. 86279), obtained from Persia through the Division of Plant Exploration and Introduction of the Bureau of Plant Industry, showed by far the most resistance (fig. 4). The resistance of this variety seems to be determined by certain growth characters, which help to hold the thrips population to a minimum, and perhaps by anatomical and physiological characters, which help the plant to withstand injury. The shape of the leaves is probably of importance in restricting the thrips population. In most varieties the leaf blades have a flat side; in opposite leaves these sides are face to face and the young leaves are closely pressed together so that the larvae are protected against insect enemies and adverse weather conditions. In White Persian the leaves are almost circular in cross section and protection is reduced to a minimum. The wide angle between the two innermost leaves, especially in the young plant, is another White Persian character that helps to restrict the thrips population by reducing their protection to a minimum. Still another character, probably of some importance, is the greater vertical distance between the leaf blades, each new leaf extending its sheath farther beyond the one encircling it than in other known cultivated varieties. This habit of growth produces an extremely long sheath column.

Figure 4.—Thrips-resistant onions. The three rows to the left are the variety White Persian (P. I. 86279); to the right are Australian Brown. Note the serious damage done by thrips to the latter variety and the freedom of the White Persian from injury. (From Jones, Bailey, and Emsweller, *11*.)

If commercial varieties of onions had these leaf characters the thrips population per plant would be reduced to a minimum and it would be possible to secure more efficient control by spraying or dusting. The shape and habit of leaf growth in the White Persian help to restrict the number of thrips; other characters help the plants to withstand injury, but these are as yet undetermined. Maughan and MacLeod (*16*) are of the opinion that avoidance of the plant by the thrips, the angle of contact of the leaves, the stage of growth of the plants, the ability of the plant tissues to recover from injury, and probably other influences have a bearing on resistance.

CROSSES BETWEEN SPECIES

The Nebuka type of *Allium fistulosum* has very little commercial importance in the United States at the present time, but because of its resistance to various diseases, insects, and adverse climatic conditions it has become a valuable source of breeding material. Crosses have been made between Nebuka and various important commercial varieties of *A. cepa* by Emsweller and Jones (*3*), with the object of incorporating certain resistance factors possessed by Nebuka into commercial varieties of *A. cepa*. This species cross is rather difficult to make, but with the aid of flies considerable numbers of first-generation hybrid seed have been produced.

The Nebuka types are nonbulbing; the hybrids between them and *Allium cepa* are intermediate in bulbing habit (fig. 5). Nebuka is a perennial; *A. cepa* is a biennial; the hybrids between the two are perennials, the tops remaining erect and the plants continuing to grow

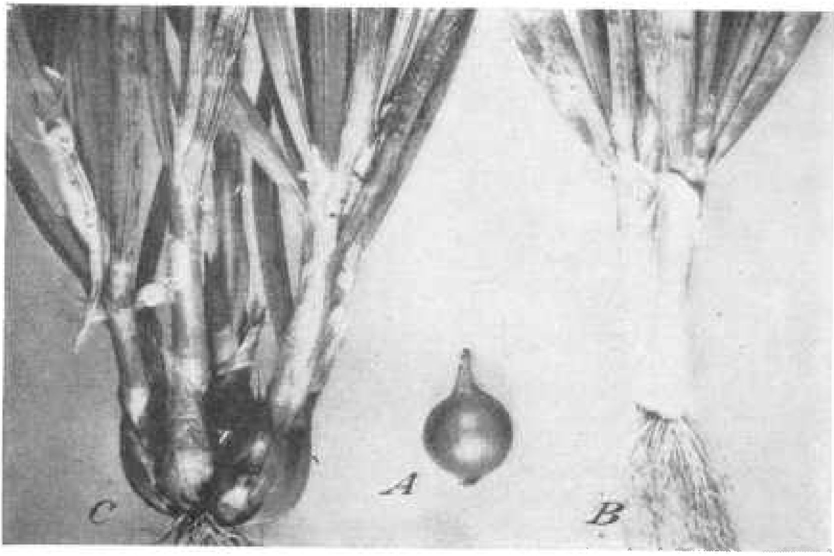

Figure 5.—*A*, Commonly cultivated bulbing type of onion, *Allium cepa*, variety Yellow Globe Danvers; *B*, Japanese onion, *A. fistulosum*, Nebuka type; *C*, first-generation hybrid between the two. This species cross gives great promise for breeding onions resistant to diseases and other adverse conditions (*3*).

as long as weather conditions are favorable. Although seed is produced in abundance by Nebuka, the plants continue to form divisions at the base, and these can be used for propagation. In date of flowering the hybrids are intermediate between the two parents. Nebuka is usually in bloom 6 or 7 weeks before *A. cepa*. Blossoming occurs irregularly over the entire inflorescence throughout the flowering period in *A. cepa*, but in Nebuka the terminal flowers open first and blossoming proceeds progressively toward the base. In the hybrid the terminal flowers are the first to open, although with less precision than in Nebuka; then a wave of opening extends toward the base, but this does not terminate the blooming of the umbel, for blossoming then continues for a time over the entire inflorescence as it occurs in *A. cepa*. In *A. cepa* the perianth becomes fully expanded; in *A. fistulosum* it remains erect; the hybrid resembles the *fistulosum* parent very closely. In the Nebuka varieties the leaves are circular in cross section, whereas in most varieties of *A. cepa* the leaf blade is semicircular; in the hybrid the semicircular type of leaf is dominant. Under similar growing conditions the hybrids show more vigor than either of the parents. They multiply rapidly by subdivisions at the base, and should be able to increase and perpetuate themselves under natural conditions. The hybrids are practically self-sterile; they are, however, useful as pollen parents for back crossing to both *A. cepa* and *A. fistulosum*. When the percentage of functional reproductive bodies is very small, normal sperm cells are naturally more numerous than normal egg cells, because of the much larger total number produced.

PREMATURE SEEDING AND FREEZING INJURY

Premature seeding (bolting) occasionally causes heavy losses in the early crop of the South and in those districts where an intermediate crop is grown from dry sets or transplants. In central California the percentage of bolting is high when a cool spring follows a warm fall. A warm fall causes a large plant to develop. This size and cool spring weather provide the proper combination of conditions for bolting, according to Jones, Poole, and Emsweller (*13*). Because of the lower temperatures prevailing along the central California coast, bolting is more prevalent there than in the interior valleys, making it an ideal place to select and breed nonbolting strains that may be useful elsewhere. The difference in bolting habit between varieties is clearly brought out by comparable plantings made in five locations in California during the season 1934–35. A few of the varieties, with the percentages of bolting, follow: Babosa, 73; Lord Howe Island, 66; Earliest Express, 66; Early Grano, 63; Blood Red Rocco, 51; White Italian Tripoli, 42; California Early Red, 19; and Italian Red, 17. A selection out of Stockton Yellow Globe, strain 36–40, gave only 2 percent of bolters, while a selection out of Stockton Yellow, strain 21–1–3–4–S_3, inbred for six generations, was entirely nonbolting. These highly nonbolting strains are being used in crosses to incorporate this character into varieties that are prone to seed prematurely when conditions favor.

Magruder and Hawthorn (*15*) found varietal differences in resistance to freezing injury, the soft-textured types of onion, such as Yellow Bermuda, Crystal Wax, California Early Red, Extra Early Yellow, and Italian Red, being the most susceptible.

GARLIC

The culture of garlic (*Allium sativum*), like that of onion, dates back to time immemorial. Vavilov (*21*) gives middle Asia as the primary center of origin and the Mediterranean region as the secondary center. From these centers the culture of the plant has become worldwide. It is highly prized for seasoning. Large collections of foreign varieties of garlic have been secured by several States through the Division of Plant Exploration and Introduction. These varieties vary widely in such characters as number, size, keeping quality, color, and pungency of the cloves, time of maturity, yield, resistance to thrips, and extent of flower development. On some varieties flower stems have never been observed to develop; on others they reach a height of 4 to 6 feet and contain umbels with a thousand or more flowers; and between these two extremes there seem to exist all possible gradations. For some reason, at present unknown, all varieties fail to produce seed. Even on the profusely blooming Spanish and Creole types seeds have never been observed. Because of the lack of sexual reproduction, improvement must be secured entirely through the selection of bud mutations.

CYTOLOGY AND GENETICS OF THE ONION [2]

THE onion has long been used as a source of material for studying the behavior of the somatic and meiotic chromosomes. Emsweller and Jones (*4*) studied the morphology of the chromosomes of the two species *Allium cepa* and *A. fistulosum*, to develop a method by which the chromosomes of a genom could be identified, avoiding so far as possible the use of total chromosome length. Chromosomes were observed at the first division of the microspore, at which time they are well spaced and only one of each pair is present. The length of any individual chromosome when measured in different cells is not constant because of lack of uniformity in stage of contraction and in fixation. The constriction region is assumed to be located at a definite point on the chromosome, making it possible at least at late metaphase to recognize two arms, and a constant index figure can be calculated by dividing the length of the short arm by that of the long arm. Emsweller and Jones (*5*) have shown also that the type of chiasma is gene-controlled. In *A. fistulosum* the chiasmata, at the first metaphase, are localized at the constriction region, while in *A. cepa* the chiasmata are placed at random. In the first generation the chiasmata were at random as in the *cepa* parent. In back crosses to *A. fistulosum* chiasmata were localized in 10 plants and at random in 7, indicating that the difference in type of chiasma is controlled by a single gene, the localized type being recessive.

In a genetic analysis of the three bulb colors, red, yellow, and white, commonly present in the cultivated onion, Rieman (*20*) found that it was necessary to postulate five different genes to account for the results secured—*I*, a gene for incomplete inhibition of color; *i*, a gene allowing expression of color; *W*, a gene for red pigment; *Wy*, a gene for yellow pigment; and *w*, a gene for white. The gene inhibiting color, *I*, is dominant to its recessive allelomorph, *i*. The heterozygous factor pair, *Ii*, produces red-necked and cream-colored bulbs in the presence of the color genes *W* or *Wy*. The latter and the factor pair *Ii* are inherited independently. The gene for red, *W*, is dominant to the gene for yellow, *Wy*, and the gene for white, *w*. The color genes are considered to be multiple allelomorphs.

Rasmusson (*19*) observed several abnormalities in chlorophyll development, white, yellow, chlorina, and T-chlorina. The white and yellow seedlings soon die. The chlorina form is yellowish at first but later may become greenish. The T-chlorina is somewhat paler in color than the chlorina and soon perishes. Some green plants when selfed yielded progeny in the theoretical green to white ratio of 15:1. Green and yellow, green and chlorina, and green and

[2] This section is written primarily for students and others professionally interested in genetics or breeding.

T-chlorina in each case occurred in a ratio of 3:1, but in some cases green and chlorina were in a ratio close to 15:1. Green:chlorina:white occurred in the ratio of 9:3:4, as did green:chlorina:yellow.

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